
NOVAFABRICIA BRUNNEA (HARTMAN, 1969), NEW COMBINATION, WITH AN UPDATE ON RELATIONSHIPS AMONG FABRICIINAE TAXA (POLYCHAETA: SABELLIDAE)

KIRK FITZHUGH¹

ABSTRACT. The fabriciini sabellid species, *Fabricia brunnea* Hartman, 1969, from central California, is assigned to the genus *Novafabricia* Fitzhugh, 1990, based on information provided by recently collected specimens. In particular, thoracic notosetal pseudospatulate setae were found to be limited to setigers 3–5, a feature not ascertainable from the type series. Support for this change comes from a cladistic analysis involving *N. brunnea* and other Fabriciinae genera and species. The number of *Novafabricia* species is raised to at least seven. As part of this analysis, the status and relationships of the monotypic genus, *Pseudofabricia* Cantone, 1972 (type species *P. aberrans*), *Novafabricia bilobata* Martin and Giangrande, 1991, and *Augeneriella alata* Hartmann-Schröder, 1991, are evaluated. Based on the original description, *A. alata* is a member of the undescribed taxon “Genus A” (*sensu* Fitzhugh, 1989). Results of the analysis support the recognition of *Pseudofabricia* and the generic placement of *N. bilobata*. Cladistic relationships among the seven species of *Novafabricia*, including *N. brunnea*, are analyzed and discussed. A key to *Novafabricia* species is provided.

INTRODUCTION

As part of my recent revision (Fitzhugh, 1990a) of the genus *Fabricia* Blainville, 1828, I included a partial redescription of *Fabricia brunnea* Hartman, 1969, based on syntype material from Moss Beach, central California. At that time, I regarded this species as *incertae sedis* as the distribution of thoracic notopodial pseudospatulate setae were neither indicated by Hartman (1969) nor could it subsequently be determined from the syntypes, most notosetae having been broken off. The purpose of the present paper is, in part, to redescribe this species based on recent material.

My revision (Fitzhugh, 1990a) of *Fabricia* limited the taxon to a single species, *Fabricia stellaris* (Müller, 1774), including several subspecies of questionable status. Given the evidence at hand, I suggested that such *incertae sedis* species as *F. brunnea* and *F. oregonica* Banse, 1956, would likely be shown to be members of other genera. As such, I noted that *Fabricia* might very well be monotypic, not allowing definition of the genus in terms of synapomorphy. Taking this situation into account and in conjunction with results from recent cladistic analyses (i.e., Fitzhugh, 1991a, 1992b) of Fabriciinae genera (*sensu* Fitzhugh, 1991a), the generic placement of *F. brunnea* must be judged relative

to other fabriciini taxa. This is accomplished here by extending the cladistic analyses of fabriciini genera and species by Fitzhugh (1991a, 1992b) to include *F. brunnea*.

As part of this analysis, validity of the monotypic genus, *Pseudofabricia* Cantone, 1972, can now be assessed as a result of the redescription of *P. aberrans* by Giangrande and Cantone (1990). The original description of this species was based on specimens lacking a branchial crown, and the description of setal forms was too incomplete to have allowed inclusion of the species in earlier cladistic analyses. Attention is also given here to the species *Novafabricia bilobata* Martin and Giangrande, 1991, again for the purpose of confirming the generic placement of this species. Also of relevance to this analysis is a preliminary examination of the generic status of *Augeneriella alata* Hartmann-Schröder, 1991.

Material examined for this study was either obtained from or has been deposited in the Allan Hancock Foundation Polychaete Collection of the Los Angeles County Museum of Natural History (LACM-AHF).

Novafabricia brunnea (Hartman, 1969), new combination

Fabricia brunnea Hartman, 1969:695–696, figs. 1–5; Fitzhugh, 1990a:9–12, figs. 2–4.

1. Invertebrates Section, Los Angeles County Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007.

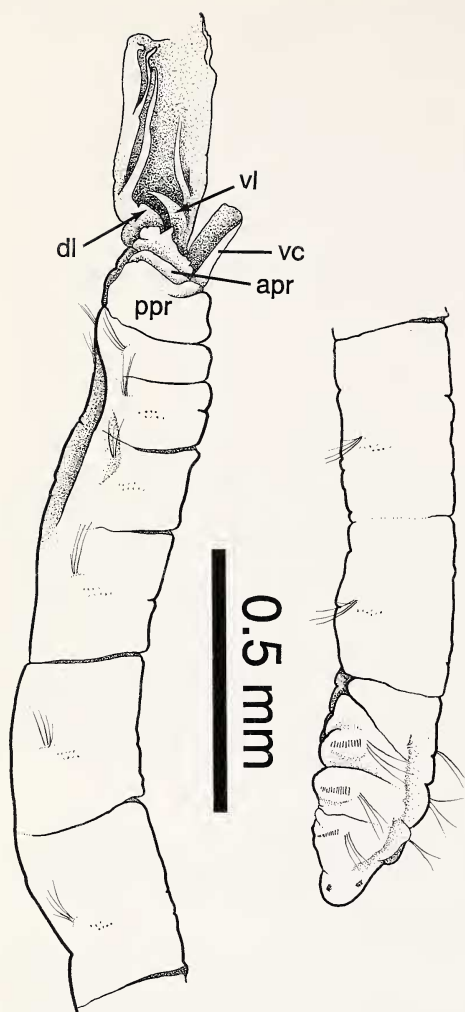


Figure 1. *Novafabricia brunnea* (LACM-AHF 1651). Entire animal in lateral view (right side; right half of branchial crown removed); figure is split between setigers 6 and 7. Abbreviations: apr, anterior peristomial ring; vc, ventral lobe-like extension of anterior peristomial ring; dl, dorsal lip; ppr, posterior peristomial ring; vl, ventral lip-like process.

MATERIAL EXAMINED. California, San Luis Obispo County; 5 complete and 1 incomplete (branchial crown missing) specimens (LACM-AHF 1651). Syntypes of *Fabricia brunnea* (LACM-AHF 3380), 12 specimens.

DESCRIPTION. All specimens in good condition with 8 thoracic and 3 abdominal setigers. Total length ranges from about 2.0 to 3.0 mm, branchial crown comprises about 0.5 mm of this length. Three pairs of radioles with filamentous distal ends of same width as pinnules. Each radiole with 5–6 pairs of pinnules, all terminating at about same height as radioles. Dorsal lips low, distally rounded; inner margin distinctly fused to most proximal pinnule of dorsal radiole. Ventral lip-like process present

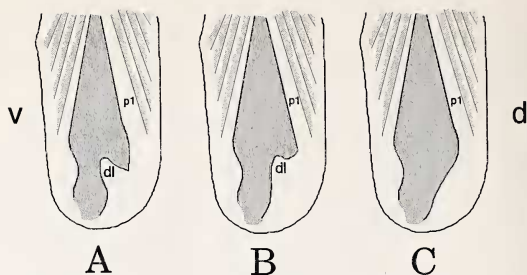


Figure 2. Slightly schematic view of the inner margin of the branchial crown, indicating possible states of dorsal-lip development in fabriciina taxa (cf. character 2, Table 2): A, dorsal lip as a triangular lobe, with dorsal margin well separated from proximalmost pinnule of dorsal radiole; B, dorsal lip with dorsal margin fused with proximalmost pinnule; C, dorsal lip absent. Abbreviations: d, dorsal body margin; dl, dorsal lip; pl, proximalmost pinnule of dorsal radiole; v, ventral body margin.

at base of most proximal pinnule of ventral radiole. Body cylindrical, anterior and posterior ends slightly tapered. Peristomial eyes dark gray, rounded to crescentic, obscured by body-wall pigment; pygidial eyes black, rounded. Anterior margin of anterior peristomial ring a low ridge dorsally and laterally; ventrally a broad, tongue-like lobe, lateral margins only slightly tapered, distally rounded, about 3.5–4 times length of remainder of anterior ring. Anterior peristomial ring (excluding ventral lobe) distinctly narrower than posterior ring. Posterior ring about 2–2.5 times longer than anterior ring. Annulation between rings distinct except along mid-dorsum. Setiger 1 about same width as posterior peristomial ring, wider than long; setigers 2–6 or 7 successively longer, setiger 5 about as wide as long; setiger 8 about same length as setiger 6. Setiger 9 about one-half length of setiger 8; setigers 10–11 successively shorter. Pygidium roughly triangular, rounded, about same length as setiger 11. Superior thoracic notosetae elongate, narrowly hooded; 5–6 per fascicle. Inferior thoracic notosetae with pseudospatulate setae in setigers 3–5; 1 per fascicle; other setigers with elongate, narrowly hooded setae. Abdominal neurosetae modified, elongate, narrowly hooded; 2–4 per fascicle. Thoracic acicular uncini in single or irregular double rows; 6–9 per fascicle; large tooth above main fang; hood present. Abdominal uncini with 5–6 teeth in profile, 4–5 teeth per row; manubrium twice as long as dentate region; manubrium constricted below dentate region, slight proximal expansion to rounded or quadrangular base; 10–13 per fascicle. Entire or proximal half of branchial crown light brown; peristomial rings and setigers 1–2 dark brown, pigmentation diminishing in posterior thoracic setigers; remaining setigers cream colored. Tube material absent; no brooding observed. Methyl green staining produces no distinct patterns.

DISTRIBUTION AND HABITAT. Central California, San Mateo County, Moss Beach, tide pool

Table 1. Current generic distributions of species described in *Augeneriella*.

Species currently recognized as members of <i>Augeneriella</i> (<i>sensu</i> Fitzhugh 1989, 1990e)	<i>Augeneriella</i> species assignable to "Genus A" (<i>sensu</i> Fitzhugh, 1989)
<i>A. hummelinki hummelinki</i> Banse, 1957	<i>A. dubia</i> Hartmann-Schröder, 1965
<i>A. hummelinki indica</i> Banse, 1959	<i>A. cf. dubia</i> (<i>sensu</i> Rouse, 1990)
<i>A. lagunari</i> Gitay, 1970	<i>A. alata</i> Hartmann-Schröder, 1991
<i>A. bansei</i> Hartmann-Schröder, 1986	
<i>A. pectinata</i> Fitzhugh, 1990e	
<i>A. basifurcata</i> Fitzhugh, 1990e	
<i>A. mossambica</i> (Day, 1957)	

among other sabellids (type locality); San Luis Obispo County, Montana de Oro State Park (35°16'16"N, 120°53'15"W), small cove adjacent to recreational area, exposed rock bench at low tide, in crevices among clumps of dense, low-growing green algae.

In addition to the type specimens, Hartman (1969: 693) also includes in *Fabricia brunnea* some of the specimens identified as *F. sabella* (*non* Ehrenberg, 1836) by Berkeley (1930) from Nanaimo, British Columbia, Canada. While I have not pursued this matter, it appears likely that Hartman did not base this conclusion on an actual examination of these specimens but, instead, relied on illustrations in Berkeley's paper, leaving open the question of such a northern distribution.

REMARKS. With the placement of *Fabricia brunnea* in *Novafabricia* Fitzhugh, 1990, the latter genus now contains at least seven species (e.g., Table 3, Fig. 3). The status of *N. gerdi* (Hartmann-Schröder, 1974) as a possible junior synonym of *Fabricia bansei* Day, 1961, has yet to be resolved (Fitzhugh, 1990d:12–13). Support for this new combination comes from the cladistic analyses presented below. In short, the features determining the generic placement of *Novafabricia brunnea* include the presence of pseudospatulate setae in setigers 3–5, also seen in *N. gerdi*, *N. infratorquata* (Fitzhugh, 1983), and *N. triangularis* Fitzhugh, 1990, and the reduced condition of dorsal lips, which is the synapomorphy defining the genus (see below).

The specimens of *Novafabricia brunnea* described here are virtually identical to the syntypes except that the former have a darker pigmented anterior end. While the ventral lobe of the anterior peristomial ring shows the same pronounced elongation (Fig. 1) seen in *N. chilensis* (Hartmann-Schröder, 1962), the distribution of pseudospatulates is different (setigers 3–6 in *N. chilensis*), as is the dentition pattern in abdominal uncini (cf. Fitzhugh, 1990d). Both species do, however, show the same ventral lip-like outgrowths at the bases of the ventralmost radioles (Fitzhugh, 1990a:fig. 3B, 1990d: fig. 6B; Fig. 1).

Development of the dorsal lips also appears to be slightly greater in *Novafabricia brunnea* (Fig. 1; Fitzhugh, 1990a:fig. 3B) than is seen in *N. chilensis* (Fitzhugh, 1990d:fig. 6B). For example, I originally

noted (Fitzhugh, 1990a:12) that in *N. brunnea* the "dorsal lips are not as well developed as those of *Fabricia stellaris*, but are more distinct than what is seen in [other species of *Novafabricia*]." Unfortunately, this generalization is not sufficient to describe any particular dissimilarities or structural relationships between dorsal-lip forms in Fabriciinae taxa.

At this time, three states can be recognized among Fabriciinae taxa for dorsal lips (Fig. 2): (1) well-developed, triangular lobes that are distinctly separated from the dorsalmost radioles by a deep, V-shaped notch (Fig. 2A; e.g., *Fabricia*, *Fabriciola* Friedrich, 1939, *Augeneriella* Banse, 1957); (2) poorly to relatively well-developed ridges that are distinctly fused to the most proximal pinnule of the dorsal radioles, leaving only a shallow, U-shaped groove between the lip and pinnule (Fig. 2B; e.g., *Novafabricia*, some species of *Pseudofabriciola* Fitzhugh, 1990); or (3) dorsal lips are completely absent (Fig. 2C; e.g., *Fabricinuda* Fitzhugh, 1990). Distinguishing dorsal lips on the basis of separation from the dorsal radioles provides a more definite means of identifying different states.

A REAPPRAISAL OF CLADISTIC
RELATIONSHIPS AMONG
FABRICIINAE TAXA

Cladistic relationships among fabriciin taxa have recently been analyzed at several hierarchical levels (Fitzhugh, 1991a, 1991b, 1992a, 1992b) subsequent to results of a cladistic analysis of Sabellidae (*sensu lato*) genera by Fitzhugh (1989). As a result of a series of revisions of fabriciin genera (i.e., Fitzhugh, 1990a, 1990b, 1990c, 1990d, 1990e), I examined (Fitzhugh, 1991a) relationships among most fabriciin taxa, the results of which support the monophyly of all included genera. A similar analysis was later performed (Fitzhugh, 1992b) with the inclusion of *Monroika africana* (Monro, 1939) and a new genus and species from Australia, *Parafabricia ventricingulata* Fitzhugh, 1992. With the addition of several new species as well as redescriptions of some older species, further work on cladistic relationships at the specific level has been carried out for *Pseudofabriciola* (Fitzhugh, 1991b; Fitzhugh et

Table 2. Characters and states used to determine cladistic relationships of Fabriciinae taxa. State "0" is plesiomorphic based on out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

1. Ventral filamentous appendages: (0) absent; (1) non-vascularized, unbranched; (2) vascularized, unbranched; (3) vascularized, branched.
2. Dorsal lips: (0) well-developed, triangular lobes, with dorsal margins well separated from proximalmost pinnules of dorsal radioles; (1) with dorsal margins fused with proximalmost radioles, forming low to moderately narrow ridges; (2) absent.
3. Position of branchial crown: (0) extends over entire anterior end; (1) shifted dorsally somewhat; (2) extensively shifted dorsally.
4. Branchial lobe shape: (0) wide and short; (1) narrow and elongate and/or with a peduncle-like process.
5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a narrow lobe; (1) low membranous collar; (2) membranous collar low dorsally and laterally, higher ventrally; (3) very high membranous collar of even width; (4) very high membranous collar that flares anteriorly; (5) low ridge dorsally and laterally, ventrally as a broad lobe; (6) low ridge dorsally and laterally, ventrally as a tongue-like lobe; (7) low ridge all around; (8) low ridge all around except for dorsolateral lobes.
6. Middorsal collar condition: (0) separate; (1) entire and distinctly grooved; (2) entire and surface smooth.
7. Middorsal collar margin: (0) separate; (1) entire; (2) notched.
8. Dorsolateral incisions on anterior margin of anterior peristomial ring collar: (0) absent; (1) present.
9. Anterior peristomial ring dimensions: (0) wider than long; (1) at least as long as wide.
10. Peristomial eyes in lateral view: (0) well developed and round; (1) poorly developed and crescentic; (2) absent.
11. Distribution of inferior thoracic pseudospatulate notosetae, in setigers 2–8: (0) absent; (1) 2–5; (2) 3–5; (3) 3–6; (4) 3–7; (5) 3–8; (6) broadly hooded, flagellate in 3–7.
12. Thoracic uncini: (0) without large tooth above main fang; (1) large tooth above main fang.
13. Thoracic uncini main fang: (0) slender; (1) swollen.
14. Abdominal uncini teeth: (0) >1 row of teeth; (1) 1 row of teeth.
15. Abdominal uncini breast: (0) oriopsis-like; (1) manubrium about 2.0 times longer than dentate region; (2) manubrium about 1.5 times longer than dentate region; (3) manubrium same length as dentate region.
16. Pygidial eyes: (0) absent; (1) present.
17. Radioles: (0) 3 or more pairs; (1) 2 pairs.
18. Body-wall spicules: (0) absent; (1) present.
19. Branchial hearts: (0) absent; (1) present.
20. Displaced pinnules (e.g., *Manayunkia*, *Monroika*): (0) absent; (1) present.
21. Thoracic uncini shape: (0) typical fabriciina shape; (1) *Manayunkia*/Genus A-type.
22. Pinnule arrangement: (0) distinctly pectinate; reduced

Table 2. Continued.

- to two (1) to four (2) pinnules at bases of branchial lobes.
23. Abdominal neuropodial pin-head setae: (0) absent; (1) present.

al., 1993) and *Fabriciola* (Fitzhugh, 1992a). The present cladistic analysis is a compilation of these studies and provides the empirical basis for revising the generic status of *Fabricia brunnea*.

A taxon that has not been considered in past cladistic analyses is the monotypic genus *Pseudofabricia* Cantone. The original description of the type species, *P. aberrans*, was based on specimens lacking a branchial crown, and details of thoracic notosetal types and distributions were vague. With the discovery of complete specimens, Giangrande and Cantone (1990) have thoroughly redescribed the species. Giangrande and Cantone did, however, assume the validity of *Pseudofabricia* relative to other fabriciina genera without any rigorous analysis of the relationship of *P. aberrans* to other fabriciina species. Inclusion of *P. aberrans* in the present analysis will determine the support for recognizing this genus.

Similarly, in their description of *Novafabricia bilobata*, Martin and Giangrande (1991) placed this species in *Novafabricia* in accordance with Fitzhugh's (1990d; see also Fitzhugh, 1991a, 1992b) suggestion that monophyly of the genus rests on the reduction of dorsal lips to low, narrow ridges. This dorsal-lip condition is, however, not unique to *Novafabricia* but is commonly seen in *Pseudofabriciola* species (e.g., Fitzhugh, 1990d, 1991b; Fitzhugh et al., 1993). Thus, *Novafabricia bilobata* is included in this analysis to assess its placement in this genus.

Augeneriella alata, from the Great Barrier Reef, was recently described by Hartmann-Schröder (1991) on the basis of a single specimen characterized by the absence of peristomial and pygidial eyes, eight thoracic and four abdominal setigers, a pair of unbranched, vascularized, ventral filamentous appendages, and the anterior peristomial ring collar being ventrally developed into a broad, lip-like extension. These features, along with Hartmann-Schröder's (1991:fig. 91) illustration of thoracic uncini, clearly indicate this is a species belonging to "Genus A" (*sensu* Fitzhugh, 1989), which is in the process of being formally described (Fitzhugh and Rouse, in prep.). When originally described by Fitzhugh (1989), "Genus A" was known to comprise *A. dubia* Hartmann-Schröder, 1965, and an undescribed species from the Indian Ocean.

Hartmann-Schröder (1991) noted similarities between *A. alata* and *A. dubia*, including the presence of four (as opposed to three) abdominal setigers and the absence of peristomial and pygidial eyes, but allied these species with *A. bansei* Hartmann-

Table 3. Character-state matrix for the 43 fabriciini species based on character states presented in Table 1. Species included in the analysis for the first time are indicated in bold. *Augeneriella bansei* Hartmann-Schröder is not included since it is based on a single, incomplete specimen.

Species	Characters and states																						
											1	1	1	1	1	1	1	1	1	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Manayunkia speciosa</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0
<i>M. baicalensis</i>	2	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0
<i>M. aestuarina</i>	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1	1	0
<i>M. brasiliensis</i>	2	0	0	0	2	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	2	0
<i>M. polaris</i>	2	0	0	0	2	0	0	0	0	0	3	0	0	0	1	0	1	0	1	0	1	1	0
<i>Monroika africana</i>	2	0	0	0	2	0	0	0	0	2	2	1	0	0	3	0	1	0	1	1	0	0	0
<i>Augeneriella dubia</i>	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0
Genus A sp.	2	0	0	0	5	0	0	0	0	2	0	0	0	0	1	0	0	1	1	0	1	0	0
<i>Fabriciola baltica</i>	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>F. berkeleyi</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>F. ghardaqa</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>F. tonerella</i>	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	?
<i>F. mediaseta</i>	1	0	0	0	1	0	0	0	0	0	6	0	0	0	1	1	0	0	1	0	0	0	1
<i>F. brevibranchiata</i>	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>F. cf. berkeleyi</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	1
<i>Pseudofabriciola australiensis</i>	2	0	0	1	4	2	2	1	0	0	0	0	1	0	3	1	0	0	1	0	0	0	0
<i>P. longa</i>	0	1	0	1	3	2	1	0	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0
<i>P. incisura</i>	2	0	0	1	4	2	2	1	0	0	0	0	0	1	0	3	1	0	0	1	0	0	0
<i>P. capensis</i>	0	0	0	1	3	1	1	1	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0
<i>P. filamentosa</i>	0	?	0	1	3	2	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>P. californica</i>	0	0	0	1	3	1	1	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0
<i>P. analis</i>	0	1	0	1	4	2	1	1	0	0	0	0	0	0	3	1	0	0	1	0	0	0	0
<i>P. longipyga</i>	?	?	?	?	4	2	2	1	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0
<i>Fabricia stellaris</i>	0	0	0	0	5	0	0	0	0	0	4	1	0	0	1	1	0	0	1	0	0	0	0
<i>Pseudofabricia aberrans</i>	0	0	0	0	5	0	0	0	0	0	0	1	0	0	3	1	0	0	1	0	0	0	0
<i>Augeneriella hummelincki</i>	3	0	0	0	5	0	0	0	0	0	3	1	0	0	1	1	0	0	1	0	0	0	0
<i>A. lagunari</i>	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0
<i>A. pectinata</i>	3	0	0	0	5	0	0	0	0	0	3	1	0	0	3	1	0	0	1	0	0	0	0
<i>A. basifurcata</i>	3	0	0	0	5	0	0	0	0	1	4	1	0	0	3	1	0	0	1	0	0	0	0
<i>A. mossambica</i>	3	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
<i>Novafabricia chilensis</i>	0	1	0	0	6	0	0	0	0	0	3	1	0	1	3	1	0	0	1	0	0	0	0
<i>N. gerdi</i>	0	1	0	0	5	0	0	0	0	0	2	1	0	1	3	1	0	0	1	0	0	0	0
<i>N. infratorquata</i>	0	1	0	0	5	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0
<i>N. triangularis</i>	0	1	0	0	5	0	0	0	0	0	2	1	0	0	2	1	0	0	1	0	0	0	0
<i>N. tenuiseta</i>	0	1	0	0	5	0	0	0	0	0	1	0	0	2	1	0	0	1	0	0	0	0	0
<i>N. bilobata</i>	0	1	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
<i>N. brunnea</i>	0	1	0	0	6	0	0	0	0	0	2	1	0	0	1	1	0	0	1	0	0	0	0
<i>Parafabricia ventricingulata</i>	0	0	0	0	5	0	0	0	0	0	4	1	0	0	3	1	0	0	1	0	0	0	0
<i>Fabricinuda limnicola</i>	2	2	0	0	7	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
<i>F. bikini</i>	2	2	2	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
<i>F. trilobata</i>	2	2	1	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
<i>F. pseudocollaris</i>	2	2	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0
<i>F. pseudopalpa</i>	0	0	0	0	8	0	0	0	1	0	5	1	0	0	3	1	0	0	1	0	0	0	0

Schröder, 1986, as all these species have unbranched ventral filamentous appendages. Unfortunately, Hartmann-Schröder (1991) neither commented on nor cited my (Fitzhugh, 1989; see also Fitzhugh, 1991a, 1992b) finding that *A. dubia* is clearly a member of “Genus A” and cladistically is quite far removed from *Augeneriella*. Furthermore,

no mention was made of my (Fitzhugh 1990e) revision of *Augeneriella*, where I predicted that the presence of unbranched ventral filamentous appendages in the holotype of *A. bansei*, the only known specimen of the species, is likely an anomalous feature. Hartmann-Schröder (1991) also failed to mention or compare *A. alata* to Rouse’s (1990)

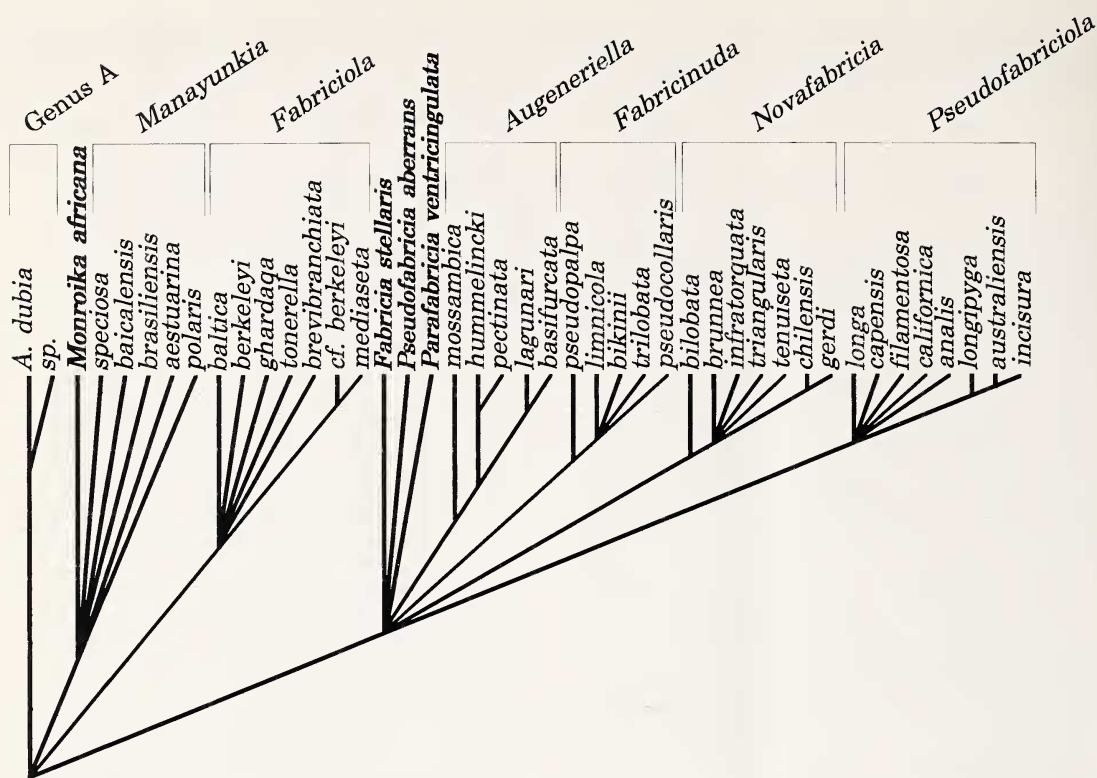


Figure 3. Strict consensus cladogram for fabriciini taxa based on 1,418 minimum-length cladograms. Monotypic genera are indicated in bold.

numerous specimens of *A. cf. dubia*, also from the Great Barrier Reef, though she does cite this paper in relation to *Oriopsis* Caullery and Mesnil, 1896. Thus, for the purposes of the present analysis, *A. alata*, although recognized as a member of "Genus A" (Table 1), is not included in the analysis since distinctions between species of that group are still being determined (Fitzhugh and Rouse, in prep.).

METHODS AND MATERIALS

The analysis includes 43 fabriciini species distributed among 11 genera. Most genera are represented by all described species except in the cases of *Manayunkia* Leidy, 1858, *Fabriciola*, and *Augeneriella* (see Fitzhugh, 1992b, for details). *Fabricia* is only represented by the nominate subspecies, *F. stellaris* (Müller, 1774; see Fitzhugh, 1990a). *Pseudofabricia aberrans* is included on the basis of preserved specimens and the description by Giangrande and Cantone (1990). Data used for the

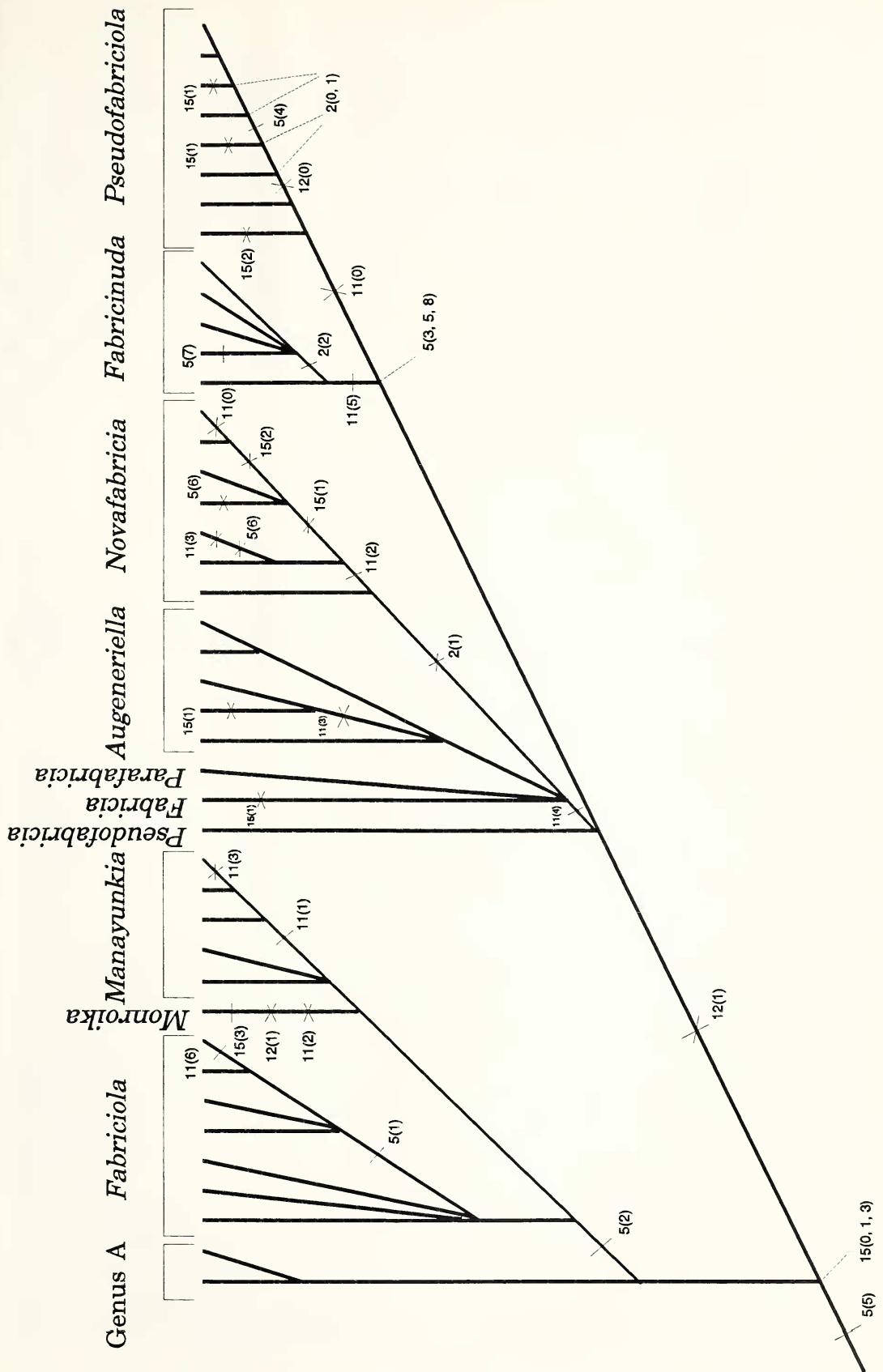
inclusion of *Novafabricia bilobata* are from the original description (Martin and Giangrande, 1991).

A total of 45 apomorphic states were used, distributed among 23 characters. Characters and states are presented in Table 2. Most characters are the same as those used by Fitzhugh (1992b), though some modifications have been incorporated as a result of studies by Fitzhugh (1991b, 1992a) and Fitzhugh et al. (1993).

States for character 2 have been modified. In previous studies, state 2(1) was described as "dorsal lips low, narrow ridges" and the plesiomorphic state as "well-developed, triangular lobes." As noted above, the dorsal lips of *N. brunnea* are slightly more developed than in other members of this genus. The separation between character states 2(0) and 2(1) is here shifted to indicate the degree of fusion with the first radioles (i.e., showing a conspicuous demarcation as opposed to being distinctly fused to the first radioles; Table 2).

The distribution of states among taxa is pre-

Figure 4. One of 1,418 minimum-length cladograms for fabriciini taxa (species indicated but not named), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. Slashes = synapomorphies, ×'s = homoplasies. Ambiguous character-state assignments are shown at nodes. See Table 2 for explanations of character states.



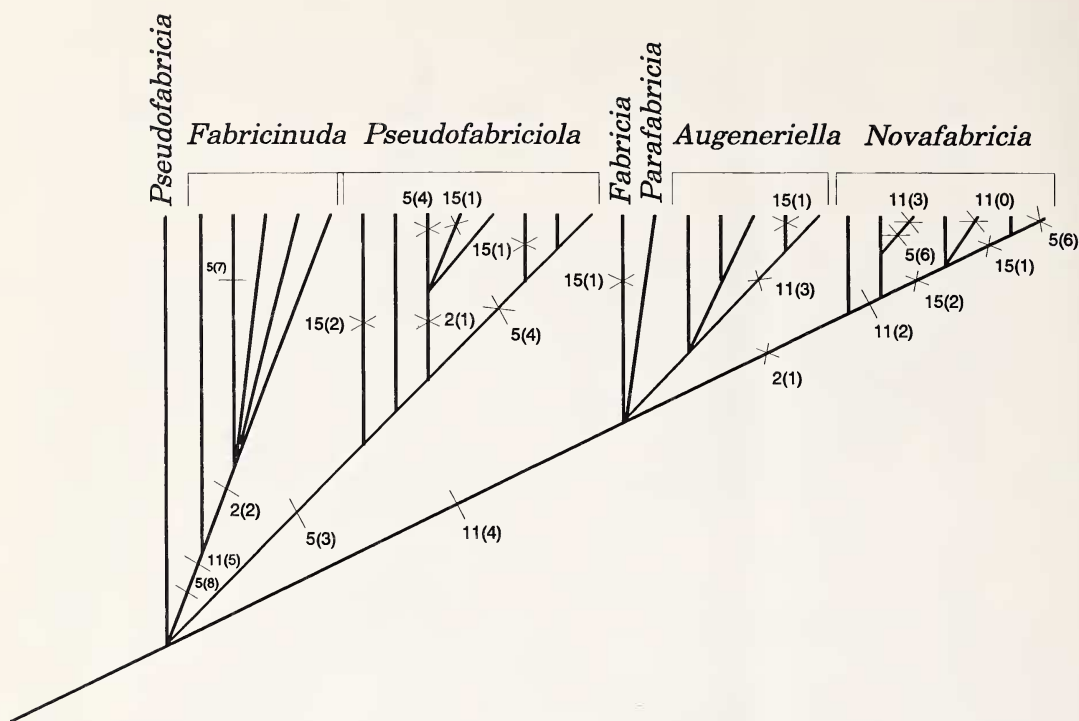


Figure 5. A portion of a cladogram of fabriciina taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

sented in Table 3. Character-state polarities are based on out-group comparisons as performed by Fitzhugh (1991a, 1991b, 1992a, 1992b), and multistate characters were treated as nonadditive.

Cladograms were constructed using the combination of commands **mhennig***; **bb*** in the computer program Hennig86, developed by Farris (1988). Lengths, consistency, and retention indices (ci and ri, respectively) and character-state transformation series were determined with the **xsteps** command using the **h** and **c** options.

RESULTS

A total of 1,418 minimum-length cladograms was produced, which is only a subset of the total number of cladograms possible using the **mhennig***; **bb*** tree-building commands; the limiting factor in this case was the amount of available computer memory. Each cladogram has a length of 68 steps, with a ci of 0.66 and ri of 0.86.

The inclusion of *Pseudofabricia* allows for a greater degree of instability at the generic level, which contributes to the larger number of cladograms (Fig. 3) than previously reported (Fitzhugh, 1991a, 1992b). Specific-level topologies appear to be roughly similar to what have been described by Fitzhugh (1991a, 1991b, 1992a, 1992b) and Fitz-

hugh et al. (1993) except in the case of *Novafabricia*, which is examined in greater detail in the analysis below. Six of the seven non-monotypic genera clearly remain monophyletic (Fig. 3). The one exception, involving the relationship of the monotypic genus *Monroikia* Hartman, 1951, to *Manayunkia*, has been analyzed and discussed in detail by Fitzhugh (1992b). The validity of the three remaining monotypic genera—*Fabricia*, *Pseudofabricia*, and *Parafabricia*—is upheld. (Fig. 3).

In all topologies, *Pseudofabricia* is a member of the clade containing *Fabricia*, *Parafabricia*, *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* (Figs. 3–6); this clade is defined by the presence of a large tooth above the main fang in thoracic uncini [state 12(1); Fig. 4]. The placement of *Pseudofabricia* within this clade is quite variable. For example, the genus can form a basal trichotomy with several genera (Figs. 4–5) or can have a more exclusive relationship to some other genera within this clade (Fig. 6).

With *Novafabricia* still defined by the reduction of the dorsal lips to low ridges [state 2(1)], the new combination *N. brunnea* is upheld, as is Martin and Giangrande's (1991) placement of *N. bilobata* in this genus (Figs. 3–6). The results of additional analyses on the relationships of *Novafabricia* species are presented below.

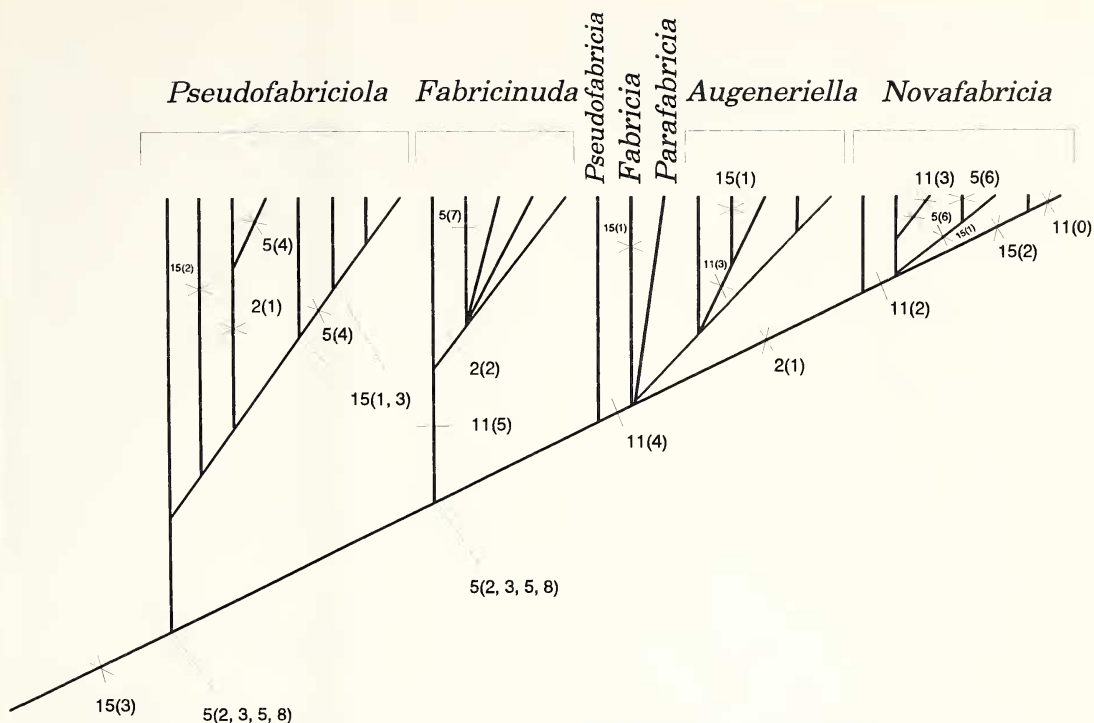


Figure 6. A portion of a cladogram of fabriciini taxa (cf. Fig. 4), illustrating one possible pattern of relationship of *Pseudofabricia* to other genera. Character-state changes are only shown for those characters indicating the monophyly of *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* relative to the monotypic genera *Fabricia*, *Pseudofabricia*, and *Parafabricia*. See Fig. 4 for explanations of character-state changes and Table 2 for descriptions of character states.

CLADISTIC RELATIONSHIPS AMONG NOVAFABRICIA SPECIES

A more detailed analysis of relationships among the seven *Novafabricia* species is presented here to examine more accurately the variability of these relationships, especially relative to results of previous analyses (e.g., Fitzhugh, 1991a, 1992b).

METHODS AND MATERIALS

The present analysis involved the seven *Novafabricia* species in the previous analysis. From the results of that latter analysis, five characters (Table 4) are instrumental in discerning relationships among *Novafabricia* species. Note, however, that the plesiomorphic state for character 11 (distribution of thoracic pseudospatulate setae) in Table 4 has been altered from what is shown in Table 2. This modification is in accord with the plesiomorphic state as determined in the previous analysis. All multi-state characters were, however, treated as nonadditive. The distribution of character states among species is presented in Table 5. Cladograms were constructed using the *ie** command in Hennig86.

RESULTS

Four minimum-length cladograms (Fig. 7) were produced using the data matrix in Table 5, each

Table 4. Characters and states used in the determination of cladistic relationships among *Novafabricia* species. Characters are numbered as in Table 1, though the general character-state polarity for character 11 is based on the cladistic results obtained from the matrix in Table 2. State "0" is plesiomorphic based on these out-group comparisons (see text). Order of multistate characters does not imply any views on transformation series.

2. Dorsal lips: (0) triangular lobes with dorsal margins well separated from first radiole; (1) dorsal margins fused with proximalmost radiole of first radiole forming low to moderate narrow ridge.
5. Anterior margin of anterior peristomial ring: (0) low ridge dorsally and laterally, ventrally as a broad lobe; (1) low ridge dorsally and laterally, ventrally as a tongue-like lobe.
11. Distribution of inferior thoracic pseudospatulate notosetae in setigers 2–8: (0) 3–7; (1) 3–5; (2) 3–6; (3) absent.
14. Abdominal uncini teeth: (0) >1 row of teeth; (1) 1 row of teeth.
15. Abdominal uncini breast: (0) manubrium same length as dentate region; (1) manubrium about 1.5 times longer than dentate region; (2) manubrium about 2.0 times longer than dentate region.

Table 5. Character-state matrix for all species of *Novafabricia* based on character states presented in Table 3.

Species	Characters and states				
	2	5	11	14	15
Outgroup	0	0	0	0	0
<i>N. bilobata</i>	1	0	0	0	0
<i>N. brunnea</i>	1	1	1	0	2
<i>N. chilensis</i>	1	1	2	1	0
<i>N. gerdi</i>	1	0	1	1	0
<i>N. infratorquata</i>	1	0	1	0	2
<i>N. tenuiseta</i>	1	0	3	0	1
<i>N. triangularis</i>	1	0	1	0	1

with a length of 9 steps and a ci and ri of 0.88 and 0.80, respectively. Among these cladograms, only the placements of *Novafabricia bilobata* and a clade containing *N. chilensis* and *N. gerdi* are stable. *Novafabricia bilobata* is the sister group to all other species by way of having thoracic pseudospatulate setae in setigers 3–7 [state 11(0)]. The *N. chilensis*–*N. gerdi* clade is defined by the presence of a single row of teeth in abdominal uncini [state 14(1)]. In three topologies (Fig. 7A–C) this clade is the sister group to the clade containing *N. infratorquata*, *N. brunnea*, *N. tenuiseta* Fitzhugh, 1990, and *N. triangularis*. In the fourth topology (Fig. 7D), the *N. chilensis*–*N. gerdi* clade forms a trichotomy with a clade containing *N. infratorquata* and *N. brunnea* and another clade with *N. tenuiseta* and *N. triangularis*.

DISCUSSION

The increased lack of resolution at the generic level as well as the larger number of cladograms produced in the first analysis as compared to what are reported in earlier studies (e.g., Fitzhugh, 1991a, 1992b) is directly related to the inclusion of *Pseudofabricia aberrans* and *Novafabricia bilobata*. Being primarily characterized by plesiomorphic features, especially the absence of thoracic pseudo-spatulate setae [state 11(0); Table 2], the placement of *Pseudofabricia* is quite unstable and allows for a larger number of topologies involving this genus and *Augeneriella*, *Novafabricia*, *Fabricinuda*, and *Pseudofabriciola* (cf. Fitzhugh, 1991a, 1992b).

As noted by Martin and Giangrande (1991), *Novafabricia bilobata* is very distinct from other *Novafabricia* species by the presence of pseudospatulate setae in setigers 3–7 [state 11(4); Table 2]. In relating *Novafabricia* species to other fabriciina taxa, the presence of character state 11(4) within *Novafabricia* has resulted in substantial changes in patterns of relationship among these species as well as resultant hypotheses of transformation series.

For example, in the analyses conducted by Fitzhugh (1991a, 1992b; Fig. 8B, C) for the then known five species, the presence of pseudospatulate setae

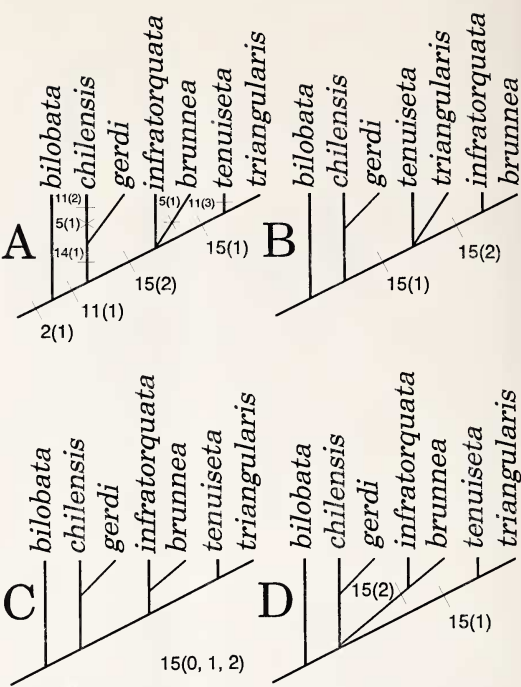


Figure 7. Possible minimum-length cladograms for *Novafabricia* species. All character-state changes are shown in A. Character-state changes in B–D are as in A except where indicated. See Fig. 4 for explanations of character-state changes and Table 4 for descriptions of character states.

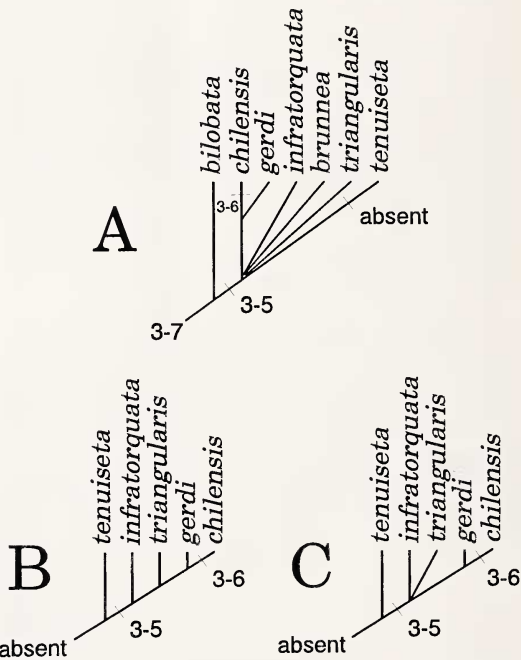


Figure 8. Past and present patterns of relationships among *Novafabricia* species, indicating the presence, distribution, and polarity of thoracic pseudospatulate setae: A, strict consensus cladogram of the four topologies in Fig. 7; B, topology from Fitzhugh (1991a:fig. 9); C, topology from Fitzhugh (1992b:fig. 5).

is a derived condition within *Novafabricia* as well as being homoplasious relative to other fabriciini genera. The nature of this transformation series resulted from the absence of pseudospatulates in *N. tenuiseta*, which was the sister group to all other *Novafabricia* species. Thus, *N. tenuiseta* displays the more general fabriciini condition of lacking pseudospatulates.

With the inclusion of *Novafabricia bilobata*, however, the transformation series for pseudospatulates is altered, as is shown in the present analysis of relationships among *Novafabricia* species (Figs. 7–8), such that the presence of pseudospatulates in setigers 3–7 [state 11(0); Table 4] is now the plesiomorphic condition for the genus. An additional result is the placement of *N. tenuiseta* at a more exclusive sister-group position by the presence of only elongate, narrowly hooded setae in setigers 2–8 [state 11(3); Table 4]. Relative to other fabriciini taxa, this setal distribution is hypothesized to be a reversal.

KEY TO SPECIES OF
NOVAFABRICIA

- 1a. Inferior thoracic notosetae of setigers 2–8 short, elongate, narrowly hooded *N. tenuiseta* Fitzhugh
- b. At least some inferior thoracic notosetae are pseudospatulate 2
- 2a. Inferior thoracic pseudospatulate notosetae limited to setigers 3–5 4
- b. Pseudospatulates in setigers 3–6 or 3–7 ... 3
- 3a. Pseudospatulates in setigers 3–6 *N. chilensis* (Hartmann-Schröder)
- b. Pseudospatulates in setigers 3–7 *N. bilobata* Martin and Giangrande
- 4a. Ventral lobe-like extension of anterior peristomial ring triangular in shape 5
- b. Ventral extension as a broad, tongue-shaped lobe *N. brunnea* (Hartman), new combination
- 5a. Abdominal uncini viewed *in situ* with prominent, single proximal row of teeth distally surmounted by 1–2 multidentate rows *N. gerdi* (Hartmann-Schröder)
- b. Abdominal uncini with at least several rows of teeth throughout 6
- 6a. Manubrium of abdominal uncini about same length as dentate region *N. triangularis* Fitzhugh
- b. Manubrium of abdominal uncini two times longer than dentate region *N. infratorquata* (Fitzhugh)

ACKNOWLEDGMENTS

Sincere thanks go to Dr. Greg Rouse, National Museum of Natural History, for sorting out the specimens of *Novafabricia brunnea* upon which part of this study is based, and for his thoughtful discussions of fabriciini systematics.

LITERATURE CITED

Banse, K. 1957. Die Gattungen *Oriopsis*, *Desdemona* und *Augeneriella* (Sabellidae, Polychaeta). *Viden-skabelige Meddelelser fra Dansk Naturhistorisk Forening* 19:67–105.

———. 1959. On marine Polychaeta from Mandapam (South India). *Journal of the Marine Biological Association of India* 1:165–177.

Berkeley, E. 1930. Polychaetous annelids from the Nainaimo district. Part 5. Ammocharidae to Myzostomidae, with an appendix on some pelagic forms from the Straits of Georgia and the west coast of Vancouver Island. *Contributions to Canadian Biology*, n.s. 6:65–77.

Cantone, G. 1972. *Pseudofabricia aberrans* n.gen. n.sp., un anellide polichete di incerta sede. *Bollettino delle Sedute della Accademia Gioenia di Scienze Naturali in Catania, Serie IV* 11:1–7.

Day, J.H. 1957. The polychaete fauna of South Africa. Part 4: New species from Natal and Moçambique. *Annals of the Natal Museum* 14:59–129.

Farris, J.S. 1988. *Hennig86 reference, version 1.5*. Distributed by the author, 41 Admiral Street, Port Jefferson Station, New York, NY 11776, 18 pp.

Fitzhugh, K. 1989. A systematic revision of the Sabellidae–Caoangiidae–Sabellongidae complex (Annelida: Polychaeta). *Bulletin of the American Museum of Natural History*, no. 192, 104 pp.

———. 1990a. A revision of the genus *Fabricia* Blainville, 1828 (Polychaeta: Sabellidae: Fabriciinae). *Sarsia* 75:1–16.

———. 1990b. *Fabricinuda*, a new genus of Fabriciinae (Polychaeta: Sabellidae). *Proceedings of the Biological Society of Washington* 103:161–178.

———. 1990c. Revision of the Fabriciinae genus *Fabriciola* Friedrich, 1939 (Polychaeta: Sabellidae). *Zoologica Scripta* 19:153–164.

———. 1990d. Two new genera of the subfamily Fabriciinae (Polychaeta: Sabellidae). *Museum Novitates*, American Museum of Natural History, no. 2967, 19 pp.

———. 1990e. Revision of the Fabriciinae genus *Augeneriella* Banse, 1957 (Polychaeta: Sabellidae). *Journal of Natural History* 24:195–218.

———. 1991a. Further revisions of the Sabellidae subfamilies and cladistic relationships among the Fabriciinae (Annelida: Polychaeta). *Zoological Journal of the Linnean Society* 102:305–332.

———. 1991b. Systematics of several fabriciini fan worms (Polychaeta: Sabellidae: Fabriciinae) previously referred to *Fabricia* or *Fabriciola*. *Journal of Natural History* 25:1101–1120.

———. 1992a. Species of *Fabriciola* Friedrich, 1939 (Polychaeta: Sabellidae: Fabriciinae) from the California coast. *Pacific Science* 46:68–76.

———. 1992b. On the systematic position of *Monroika africana* (Monro) (Polychaeta: Sabellidae: Fabriciinae) and a description of a new fabriciini genus and species from Australia. *Proceedings of the Biological Society of Washington* 105:116–131.

Fitzhugh, K., A. Giangrande, and N. Simbhora. 1993. New species of *Pseudofabriciola* Fitzhugh, 1990 (Polychaeta: Sabellidae: Fabriciinae) from the Mediterranean Sea. *Zoological Journal of the Linnean Society* (in press).

Giangrande, A., and G. Cantone. 1990. Redescription and systematic position of *Pseudofabricia aberrans*

- Cantone, 1972 (Polychaeta, Sabellidae, Fabriciinae). *Bollettino Zoologia* 57:361–364.
- Gitay, A. 1970. A review of *Augeneriella* (Polychaeta: Sabellidae) and a new species from Northern Sinai. *Israel Journal of Zoology* 19:105–109.
- Hartman, O. 1969. *Atlas of sedentary polychaetous annelids from California*. Los Angeles: Allan Hancock Foundation, 812 pp.
- Hartmann-Schröder, G. 1965. Zur Kenntnis der eulitoralischen Polychaetenfauna von Hawaii, Palmyra und Samoa. *Abhandlungen und Verhandlungen der Naturwissenschaftlichen Verein (Hamburg)* 9:81–161.
- . 1986. Teil 12. Die Polychaeten der antiborealen Südküste Australiens (zwischen Wallaroo im Westen und Prot MacDonnell im Osten). In *Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden*, ed. G. Hartmann-Schröder and G. Hartmann. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 83:31–70.
- . 1991. Teil 16. Die Polychaeten der subtropischen bis tropischen Ostküste Australiens zwischen Maclean (New South Wales) und Gladstone (Queensland) sowie von Heron Island (Großes Barriere-Riff). In *Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden*, ed. G. Hartmann-Schröder and G. Hartmann. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 88:17–71.
- Martin, D., and A. Giangrande. 1991. *Novafabricia bilobata* sp. nov. (Polychaeta, Sabellidae, Fabriciinae) from the Mediterranean. *Ophelia* 33:113–120.
- Rouse, G. 1990. New species of *Oriopsis* (Sabellidae: Polychaeta) and a new record of *Augeneriella* cf. *dubia* Hartmann-Schröder, 1965 (Sabellidae: Polychaeta) from eastern Australia. *Records of the Australian Museum* 42:221–235.

Received 14 April 1992; accepted 29 June 1993.